

BREEDING MECHANISMS IN TREES NATIVE TO TROPICAL  
FLORIDA — A MORPHOLOGICAL ASSESSMENT \*

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SOME RECENT DISCUSSION of probable speciation processes in tropical rain forest trees has centered on breeding mechanisms (Fedorov, 1966; Ashton, 1969) and has served to draw attention to our ignorance of the topic. There are no extended observations on breeding mechanisms in a wide range of tropical trees, so the subject has been discussed largely at a hypothetical level. One assumption is that since individuals of the same species tend to be widely separated in tropical rain forests, self-fertilization (autogamy) must be the rule (Fedorov, 1966). Ashton (1969), on the other hand, on the basis of observation suggests that outcrossing (xenogamy) is the rule. An extended assessment by Bawa (1973), based on controlled pollinations in a lowland semideciduous forest in Costa Rica, demonstrates a high degree of outcrossing, chiefly on the basis of a high incidence (52 per cent) of self-incompatible species. Bawa estimates that at least 75 per cent of the species have an obligate xenogamous mode of reproduction. Whether it is safe to regard these results as typical of other communities is uncertain, but they indicate interesting trends. In this context also, the ability of some bees to travel long distances in tropical environments (Janzen, 1971) is suggestive of an agent assisting outcrossing, although experimental evidence that bees cover these distances in transferring pollen has not yet been provided, nor is it likely to be done easily.

Bawa provides a lengthy discussion of the kinds of problems encountered in work of this sort. Since it is necessary to make extended observations on sizable populations of a great variety of tree species in natural environments, progress is likely to be slow. In this sense Bawa's observations represent only a pioneering venture. The practical importance of this type of work is not in doubt. For example, cultivation of avocado (*Persea americana*) is scarcely possible without a knowledge of its complex pollination mechanism, one of the few examples of the breeding mechanisms of a tropical tree which has been studied in detail. The floral mechanism of avocado is outlined by Wood (1958, p. 331) and involves dianthesis, that is, two periods of opening on successive days with an intermediate period when the flower is closed. The stage of flower development is synchronous throughout a single tree. Two types of tree, "A" and "B," are recognized whose periods of flowering are staggered

\* "Tree" is used in a rather generous sense. I include a number of native woody plants which mostly occur as tall shrubs. The selection of species is undeniably arbitrary, but certainly includes all species which would conform to a forester's definition of a tree, excluding only a few very rare species which have not been investigated.



so that cross-pollination is possible. Flowers are protogynous; in type "A" the stigmas are receptive on the morning of the first day, the flowers close in the afternoon to re-open on the afternoon of the second day; in type "B" the carpellate stage is in the afternoon of the first day, the staminate phase is in the morning of the second day. Avocado cultivation requires that cultivars in one orchard should be of both "A" and "B" type in order to permit fruit set.

The present account represents only a superficial and elementary contribution to this field, using a part of the native woody flora of South Florida. It is a preliminary assessment of kinds of breeding mechanisms of the trees of this area, based solely on floral morphology and without the complementary experiments that Bawa (1973) demonstrates are essential for a more reliable analysis. However, since I am unlikely to have the opportunity to extend this study in the required direction, the information is presented with the hope that botanists in South Florida will continue the work. Although South Florida is wholly extratropical, this study is relevant to students of tropical biology because the species represented are predominantly West Indian or circum-Caribbean in their distribution, are within their natural range, and grow in natural habitats. The uniqueness of this tree flora in the continental United States has been emphasized previously (e.g., Sargent, 1905); it represents an outlier of tropical vegetation surrounded by, and to a certain extent penetrated by, temperate tree-species of the flora of the eastern United States. Nevertheless the biological potential of this area for extended investigation goes largely unrecognized by American scientists.

Quite elementary observations are still to be made on this flora. The existence of dioecism in the genus *Coccoloba* (150 species, Polygonaceae) was not recognized clearly until described by Howard (1949) in West Indian species. Previously Lindau, a monographer of the genus, had, in ignorance of the dioecious condition in certain dried collections, based separate species on staminate and carpellate flowers of what is now known to be a single species. Two species of *Coccoloba* (*C. diversifolia* and *C. uvifera*) are native to South Florida, and quite casual observation demonstrates the essentially dioecious condition readily, albeit with the recognition that there is some additional polymorphism which requires further study.

The existence of monoecism in the commercially valuable West Indian mahogany (*Swietenia mahagoni*) seems not to have been recognized generally until described by Lee (1967) from specimens cultivated in Taiwan. Previously *Swietenia* had been described as having perfect flowers. *Swietenia mahagoni*, native in South Florida, shows monoecism clearly, in confirmation of the earlier record. The implication of this simple observation in an understanding of the breeding mechanism of *Swietenia* is significant, although the functions of the two kinds of flowers in the pollination "strategy" are (as in most monoecious species) not clear. The special case of *Swietenia* is only one example in the Meliaceae, a family which



now seems to be generally diclinous, although this fact again was not generally recognized until 1963 (see Styles, 1972).

Dioecism in populations of *Citharexylum fruticosum* native to South Florida was first described by Tomlinson and Fawcett (1972), and it is possible that again we have a large genus in which dioecism is more widespread than has hitherto been appreciated (Arechavaleta, 1902; Tomlinson, 1973).

Other examples of floral polymorphism which have been previously overlooked or neglected are described in this article. Undoubtedly yet others will be brought to light. These examples serve to demonstrate the value of the woody flora of South Florida as a potential source of information about growth characteristics of tropical trees, which is of general value to biologists (cf. also Gill & Tomlinson, 1971; Tomlinson & Craighead, 1972).

#### THE WOODY FLORA OF SOUTH FLORIDA

The area considered is that covered by Long and Lakela's "Flora" (1971), including the Florida Keys, South Florida south of Lake Okechobee, plus a coastal strip on each side of the peninsula whose limits correspond approximately to the 50° F. January isotherm (Tomlinson & Craighead, 1972). Treating this woody flora in a somewhat general sense to include a number of low shrubs which only exceptionally reach any marked stature, I include 114 species. The great majority of these (98) can be described as "tropical," since they represent species with a wider distribution in tropical America, but are, in South Florida, at the northern limit of their range. The remaining 16 species are, in contrast, "temperate," with a wider range in the eastern United States, so that in South Florida they are almost at their southern limit. These northern species are indicated by the letter N in subsequent lists.

#### METHODS

Observations have been made on fresh specimens collected mainly in the wild at flowering times, supplemented by collections from trees in cultivation (mainly at Fairchild Tropical Garden). No attempt has been made to establish the incidence of self-incompatibility by experimental procedures. Dissections of fresh flowers have been examined under a Wild M-5 stereomicroscope. Representative black-and-white illustrations of all species in the flora have been made to form the basis of a more extended publication. The illustrations which accompany the present article are, however, original.

#### RESULTS

A preliminary subdivision is made between species that show dioecism or monoecism (dicliny) and species with perfect flowers (monocliny). In



some instances the distinction is not absolute, and one group of species is best discussed under the separate category of polymorphic flowers, since perfect and imperfect flowers are found on the same tree. Within the general group of species with perfect flowers morphological or functional subcategories can be recognized, notably heterostyly and dichogamy, where there is strong indication of an outcrossing mechanism.

Within each group certain species are discussed in greater detail to supplement or substantiate the categorization. It is appreciated that my observations are based only on limited samples and may be incorrect when larger populations are sampled both within South Florida and elsewhere. It seems evident, as for example with *Acer rubrum*, that there can be differences in breeding mechanisms in different parts of the range of one species.

1. **Species dioecious** (with separate staminate<sup>1</sup> and carpellate<sup>1</sup> flowers, each kind of flower restricted to a particular individual; i.e. separate staminate and carpellate trees).

ALVARADOA AMORPHOIDES *	GYMINDA LATIFOLIA
BACCHARIS GLOMERULIFLORA * N	ILEX CASSINE
BACCHARIS HALIMIFOLIA * N	ILEX KRUGIANA
CASASIA CLUSIIFOLIA (FIGURE 2)	LAGUNCULARIA RACEMOSA *
CITHAREXYLUM FRUTICOSUM	METOPIMUM TOXIFERUM
CLUSIA ROSEA	MYRICA CERIFERA * N
COCCOLOBA LAURIFOLIA	PICRAMNIA PENTANDRA *
COCCOLOBA UVIFERA (FIGURE 1)	PISONIA ROTUNDATA
CONOCARPUS ERECTUS *	RHUS COPALLINA N
DIOSPYROS VIRGINIANA N	SALIX CAROLINIANA N
DODONAEA VISCOSA (see p. 281).	SAVIA BAHAMENSIS
DRYPETES DIVERSIFOLIA *	SCHAEFFERIA FRUTESCENS
DRYPETES LATERIFLORA *	SIMAROUBA GLAUCA
EXOTHEA PANICULATA (see p. 281)	TORRUBIA (GUAPIRA) LONGIFOLIA
FORESTIERA SEGREGATA *	ZANTHOXYLUM FAGARA
FRAXINUS CAROLINIANA * N	

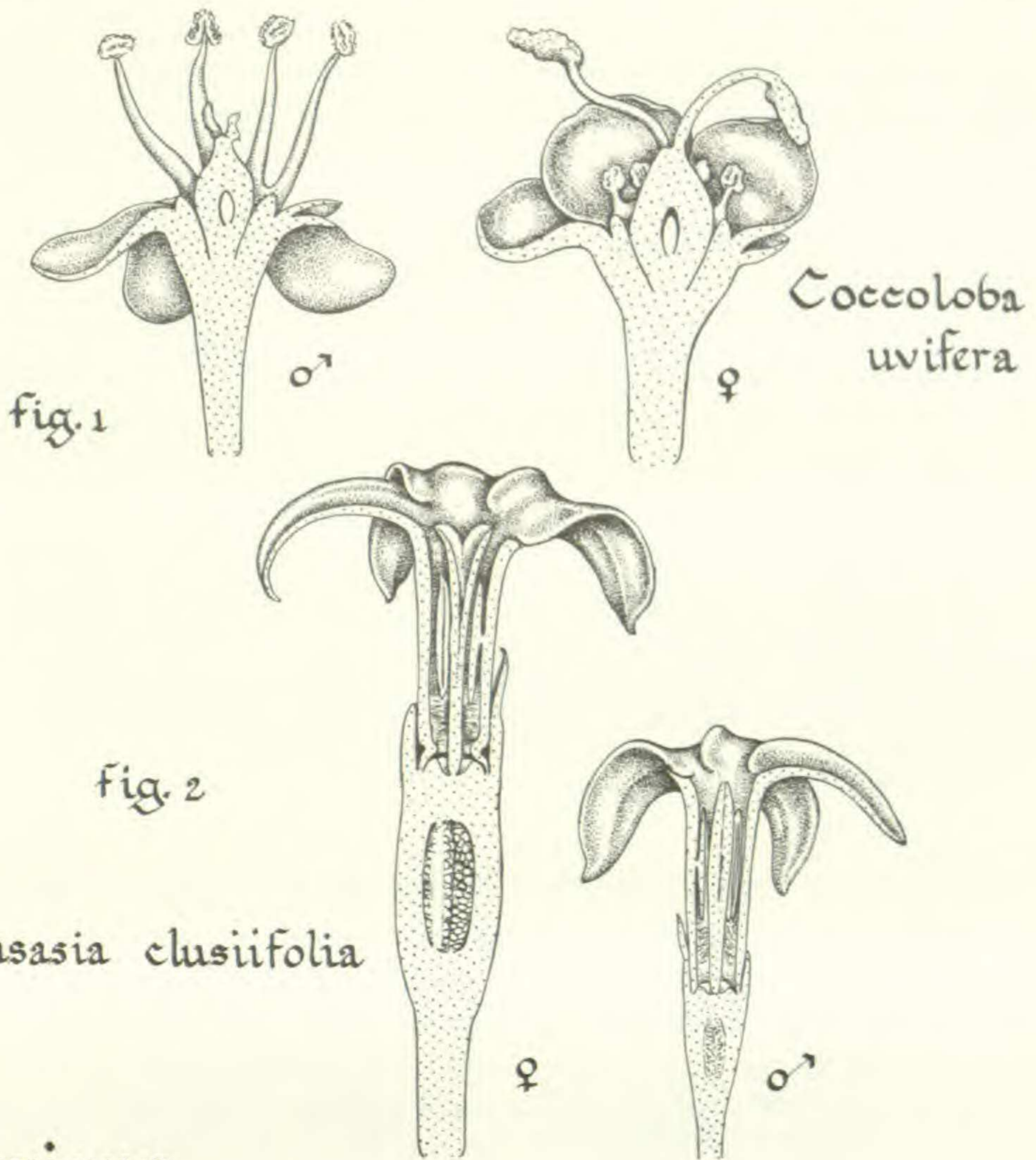
\* Probably wind-pollinated (see p. 287).

N North temperate distribution.

Most of the species in this list show evident dioecism, although in some the distinction between staminate and carpellate flowers has been overlooked until recently. *Coccoloba* species have already been mentioned. Representative staminate and carpellate flowers of *Coccoloba uvifera* are shown in FIGURE 1. The dioecious condition in *Casasia clusiifolia* (Rubiaceae) is not usually recognized, since staminate flowers may have a quite well-developed ovary (FIGURE 2). The distinction between staminate trees (without fruit) and carpellate trees (with fruit) in the field seems abso-

<sup>1</sup> The terms "male" and "female" are avoided because of the ambiguities pointed out by Thieret (1973); "staminate" and "carpellate" are used at the suggestion of Dr. C. E. Wood, Jr.





## Dioecious

FIGURES 1 and 2. EXAMPLES OF DIOECISM; flowers in longitudinal section: 1, *Cocoloba uvifera*,  $\times 6$ , staminate flower to the left, carpellate flower to the right; 2, *Casasia clusiifolia*,  $\times 1\frac{1}{2}$ , carpellate flower to the left, staminate flower to the right.

lute. Furthermore, staminate flowers are borne in groups; carpellate flowers are solitary and usually larger.

The dioecious condition in *Citharexylum fruticosum* is described by Tomlinson and Fawcett (1972).

*Clusia rosea* (Guttiferae) represents a peculiar situation. I have seen no staminate flowers, and trees (mainly in cultivation) seem to be wholly carpellate, their flowers being without functional stamens. Nevertheless, the tree produces fruit with viable seeds by which it can be propagated. Presumably we are dealing here with an example of apomixis, although this needs to be verified. Some circumstantial evidence for apomixis is the observation by Dr. C. E. Wood, Jr. (pers. comm.) that *Clusia rosea* is polyembryonic.



For some species in this list there are records of perfect flowers, as in *Conocarpus* and *Simarouba*, but in my experience staminate and carpellate flowers and trees are quite distinct. In some trees of *Laguncularia* the carpellate flowers may well have functional stamens, but this has not been verified.

The correlation between dioecism and wind-pollination will be commented upon later.

2. **Species monoecious** (with separate staminate and carpellate flowers, but these borne on the same individual; i.e. trees all of one kind).

ACER RUBRUM * N (FIGURE 3)	HYPELATE TRIFOLIATA (FIGURE 4)
CELTIS LAEVIGATA * N	MORUS RUBRA * N
CUPANIA GLABRA	QUERCUS VIRGINIANA * N
FICUS AUREA	SAPINDUS SAPONARIA
FICUS CITRIFOLIA	SWIETENIA MAHAGONI (FIGURE 5)
GYMNANTHES (ATERAMNUS) LUCIDA	TREMA MICRANTHA
HIPPOMANE MANCINELLA	TREMA LAMARCKIANA

\* Probably wind-pollinated.

N North temperate distribution.

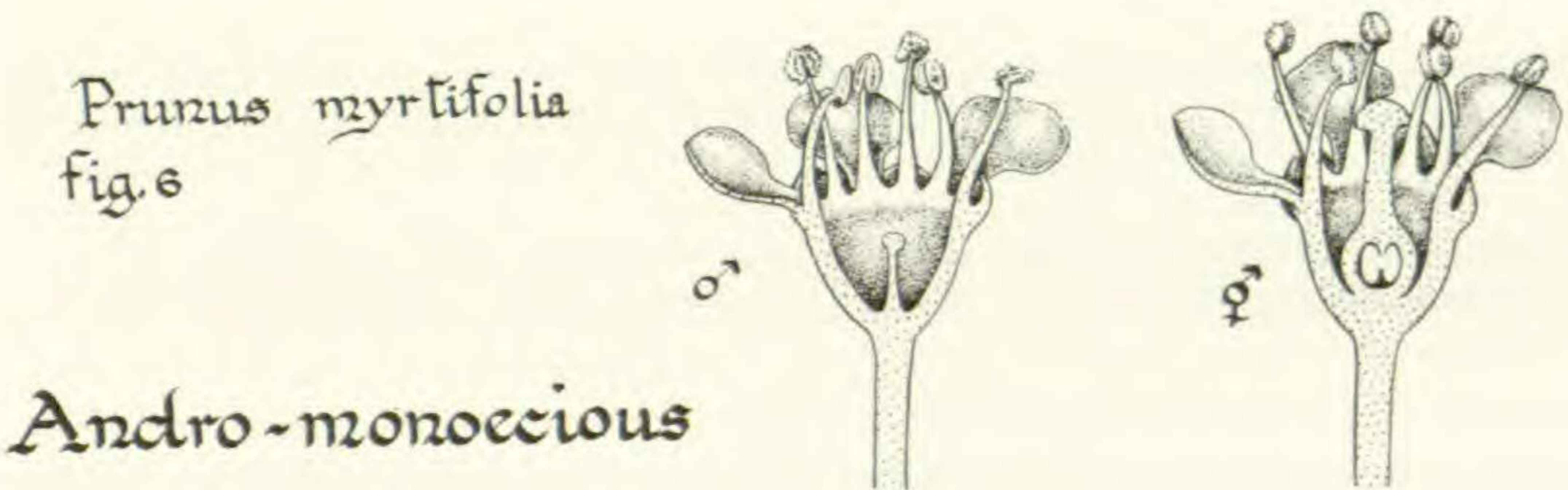
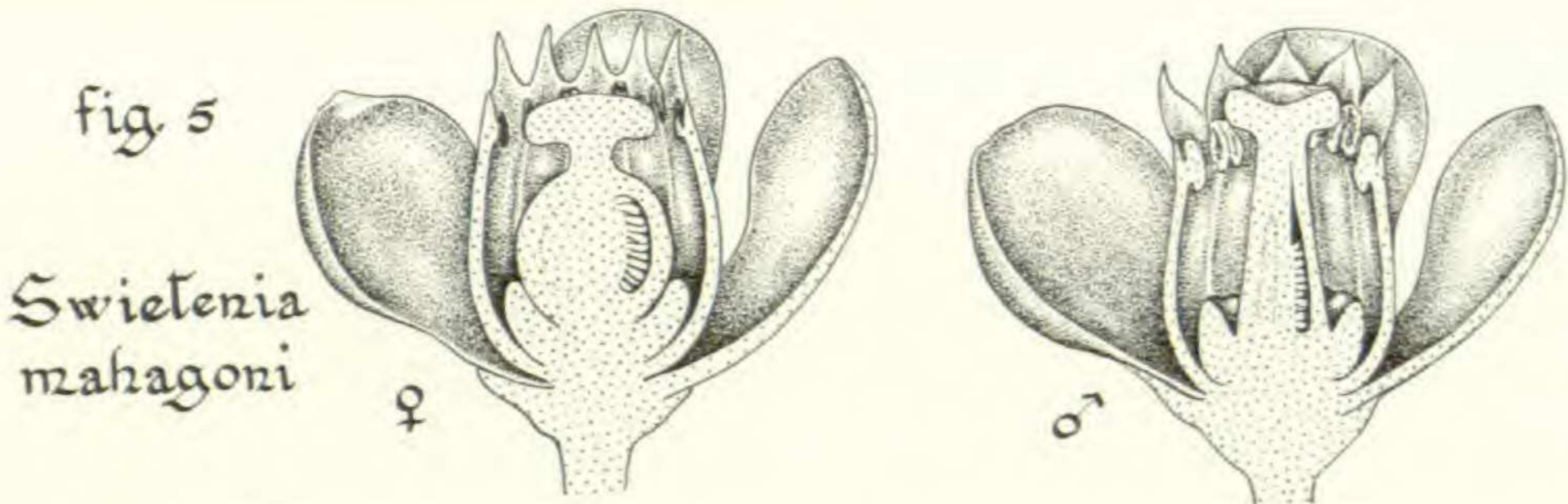
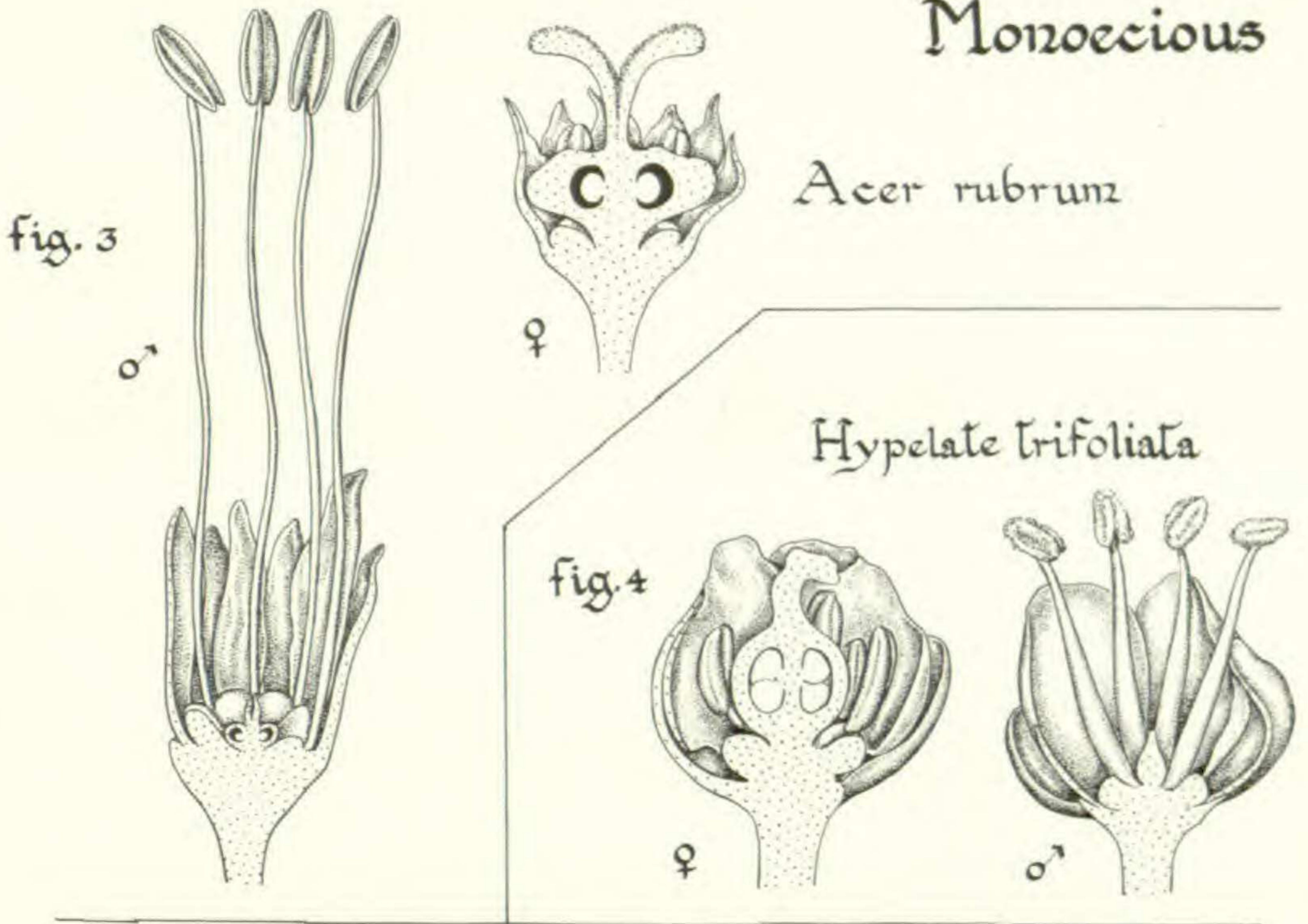
*Acer rubrum* (Aceraceae) is included unequivocally in this category. In much of its range *Acer rubrum* is regarded as dioecious (Dr. C. E. Wood, Jr., pers. comm.), but in South Florida I have seen flowers as different as those illustrated in FIGURE 3 on one individual. There is nevertheless a strong tendency toward the development of flowers which appear to be perfect. However, though well-developed stamens may seemingly be formed, one cannot be too sure that their pollen is functional. In view of the proven demonstration of physiological races in *Acer rubrum* (Perry & Wang Chi Wu, 1960), it would be unwise to generalize about its floral mechanism on the basis of a limited sample from one locality. This description of polymorphic flowers applies equally well to the two sapindaceous representatives, *Hypelate* (e.g., FIGURE 4) and *Sapindus*, which tend toward the polygamous condition of the Sapindaceae generally, often producing perfect as well as staminate and carpellate flowers. *Cupania glabra*, in the same family, is monoecious, but dioecism may be suggested where flowers of one sex predominate. Further field study might indicate that *Hypelate* and *Sapindus* would be better included in the polymorphic group where I have included two other members of the family (p. 281). *Trema* (Ulmaceae) also requires further extended observation. Trees are dioecious superficially, since they bear a preponderance of one flower type at a particular time and some trees seem to fruit more heavily than others. Incipient dioecism seems to exist here.

The remaining examples are more familiar and clear cut. The situation with regard to *Swietenia* has been described in the introduction, and representative staminate and carpellate flowers are illustrated in FIGURE 5.

The special case of monoecism in *Ficus* is discussed separately (p. 283).



Monoecious



FIGURES 3-6. EXAMPLES OF MONOECISM AND ANDRO-MONOECISM; flowers in longitudinal section: 3, *Acer rubrum*,  $\times 5$ , staminate flower to the left, carpellate flower to the right; 4, *Hypelate trifoliata*,  $\times 6$ , carpellate flower to the left, staminate flower to the right; 5, *Swietenia mahagoni*,  $\times 8$ , carpellate flower to the left, staminate flower to the right; 6, *Prunus myrtifolia*,  $\times 6$ , staminate flower to the left, perfect flower to the right.



3. Species with perfect (hermaphrodite) flowers (all flowers and individuals apparently with functional stamens and ovaries).

ACACIA FARNESIANA *	EUGENIA FOETIDA
ACACIA PINETORUM *	EXOSTEMA CARIBAEUM
AMYRIS ELEMIFERA	GOSSYPIUM HIRSUTUM
ANNONA GLABRA	GUAIACUM OFFICINALE
ARDISIA ESCALLONIOIDES	HAMELIA PATENS
AVICENNIA GERMINANS	HIBISCUS TILIACEUS
BOURRERIA CASSINIFOLIA	JACQUINIA KEYENSIS
BOURRERIA OVATA	KRUGIODENDRON FERREUM
BOURRERIA SUCCULENTA	LICARIA TRIANDRA
BUMELIA CELASTRINA	LYSILOMA BAHAMENSIS
BUMELIA RECLINATA N	MAGNOLIA VIRGINIANA N
BUMELIA (DIPHOLIS) SALICIFOLIA	MANILKARA BAHAMENSIS
BYRSONIMA LUCIDA	MASTICHODENDRON FOETIDISSIMUM
CALYPTRANTHES PALLENS	MYRCIANTHES FRAGRANS
CALYPTRANTHES ZUZYGIUM	NECTANDRA CORIACEA
CANELLA ALBA (= WINTERANA)	PERSEA BORBONIA N
CAPPARIS CYNOPHALLOPHORA	PISCIDIA PISCIPULA
CAPPARIS FLEXUOSA	PITHECELLOBIUM GUADELUPENSE *
CASSIA BAHAMENSIS	PITHECELLOBIUM UNGUIS-CATI *
CEPHALANTHUS OCCIDENTALIS N	PSIDIUM (MYRTUS) LONGIPES
CHIOCOCCA ALBA	RHIZOPHORA MANGLE †
CHRYSOBALANUS ICACO	SAMBUCUS CANADENSIS
CHRYSOPHYLLUM OLIVIFORME	(SIMPSONII) N
COLUBRINA ARBORESCENS	SOLANUM BAHAMENSE
COLUBRINA CUBENSIS	SOLANUM ERIANTHUM
COLUBRINA ELLIPTICA	SOPHORA TOMENTOSA
CROSSOPETALUM RHACOMA	SURIANA MARITIMA
ERITHALIS FRUTICOSA	TETRAZYGIA BICOLOR
ERYTHRINA HERBACEA	THESPESIA POPULNEA
EUGENIA AXILLARIS	XIMENIA AMERICANA
EUGENIA CONFUSA	VALLESIA ANTILLANA

N North temperate distribution.

\* In some Mimosoideae, e.g., *Pithecellobium (Samanea) saman* and *Albizia lebeck* (the latter a weedy tree of South Florida), the terminal flower of each inflorescence is different from the others. The native South Florida representatives of this subfamily show no such variation.

† See Footnote p. 288.

Despite the common character of perfect flowers, this group evidently includes a heterogeneous assemblage in terms of possible breeding mechanisms. Outbreeding is suggested in a number of examples by several sorts of dichogamy, with both protandry and protogyny evident in different species. Known examples where dichogamy is pronounced are listed and discussed briefly below. Field studies in other species with hermaphrodite flowers may reveal additional examples. Dichogamy itself, of course, only prevents self-pollination within individual flowers, not between the flowers of a whole plant.



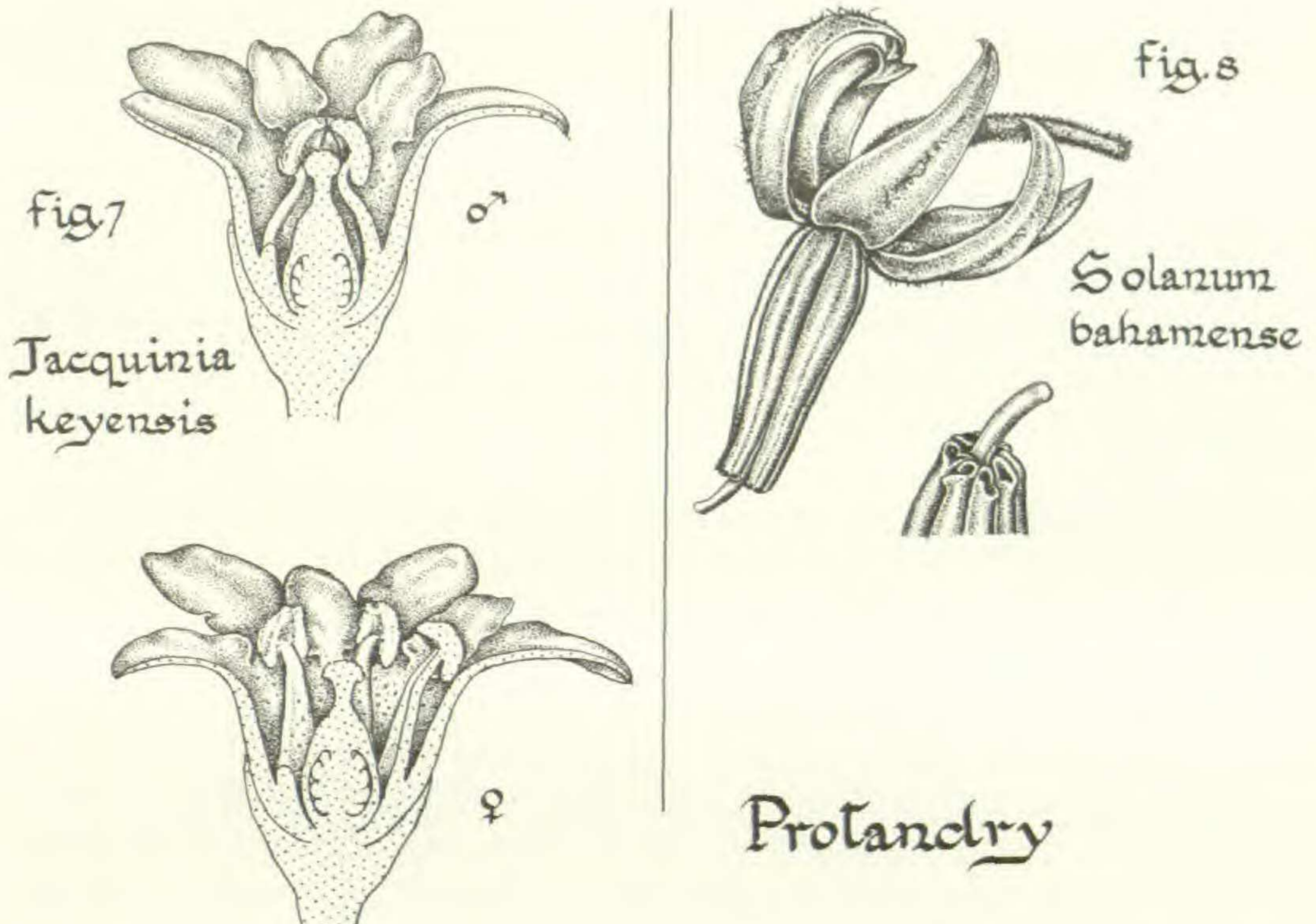
3a. *Species showing dichogamy* (anthers and stigmas of the flower maturing at different times).

(i) Protandry (stamens maturing first).

CEPHALANTHUS OCCIDENTALIS  
CHRYSOPHYLLUM OLIVIFORME  
CROSSOPETALUM RHACOMA

JACQUINIA KEYENSIS (FIGURE 7)  
SOLANUM BAHAMENSE (FIGURE 8)

*Jacquinia keyensis* (Theophrastaceae) shows pronounced protandry (FIGURE 7). In the early "male" phase, when the flower first opens, the



FIGURES 7 and 8. EXAMPLES OF PROTANDRY; flowers in longitudinal section and from the side: 7, *Jacquinia keyensis*,  $\times 4\frac{1}{2}$ , staminate phase above, carpellate phase below; 8, *Solanum bahamense*,  $\times 3$ , flower in late "carpellate" phase with stigma protruding, detail to right,  $\times 6$ , showing apical pores of anther.

stamens remain at the center of the flower, forming a small cavity within which the stigma is completely enclosed. At this time the anthers dehisce extrorsely so that pollen is displayed remote from the stigma of the same flower. In the later "female" phase the stamens bend away from the stigma which is so exposed. The same mechanism has been described by Janzen (1970) for *Jacquinia pungens*. In *Solanum bahamense* the stamens are aggregated to form a conspicuous column. Dehiscence, which is by pores, occurs while the style is short and still included within the staminal column. Subsequently the stigma is exerted by late elongation of the style. The close juxtaposition of stigma and anther pores is such that self-pollination is likely (FIGURE 8). In *Chrysophyllum* and *Crossopetalum* protandry is evident because the stigmas do not diverge until



well after the stamens have dehisced. *Chrysophyllum* (Sapotaceae) has a very simple flower structure and should be contrasted with the complex protogynous sapotaceous flowers described below.

(ii) Protogyny (stigmas maturing first).

ANNONA GLABRA	MAGNOLIA VIRGINIANA
ARDISIA ESCALLONIOIDES (FIGURE 11)	MANILKARA BAHAMENSIS
AVICENNIA GERMINANS	NECTANDRA CORIACEA
BUMELIA SALICIFOLIA (FIGURE 10)	PERSEA BORBONIA
CANELLA ALBA (FIGURE 9)	SOPHORA TOMENTOSA
FICUS AUREA	TETRAZYGIA BICOLOR
FICUS CITRIFOLIA	

The flowers of *Ardisia escallonioides* (Myrsinaceae) suggest a mechanism for promoting outcrossing that may occur in other unrelated trees in South Florida with similar general floral structure (FIGURE 11). Before the flower is fully opened the corolla lobes are rolled together to form a tube. The tip of the style protrudes through this tube and is apparently receptive; therefore, functionally the flower is carpellate. Subsequently the flower opens and pollen is presented; it is not known if the stigma continues to be receptive in this later stage. *Sophora tomentosa* seems to be essentially of this type. *Sophora* flowers are relatively unspecialized in the Faboideae (having free stamens), and their pollination mechanism seems also unspecialized compared with that of many other Leguminosae.

The Sapotaceae in South Florida show a wide range of floral mechanisms. Floral structure in some species is complicated by the existence of one or more kinds of scales on the corolla tube (either staminodes or stamen appendages). The morphology of these scales has been much discussed, but their function has been little considered. *Bumelia* (*Dipholis*) *salicifolia* is protogynous and the early carpellate phase is represented by FIGURE 10 (left), with the style protruding through the mouth of the yet unexpanded corolla tube. (This should not be confused with the late stage when the corolla has fallen and the style persists on the young fruit enclosed by the calyx.) Subsequently the corolla expands (FIGURE 10, right), but the scales bend over to form a canopy which would seem to prevent access of pollen to the stigma. Self-pollination is further minimized because the anthers dehisce extrorsely.

*Manilkara bahamensis* (Sapotaceae) is clearly protogynous, and its flowers behave much as those of *Bumelia salicifolia*, with the long style protruding from the flower essentially before it is open. This is succeeded by a staminate phase when the flower opens widely and the stamens dehisce.

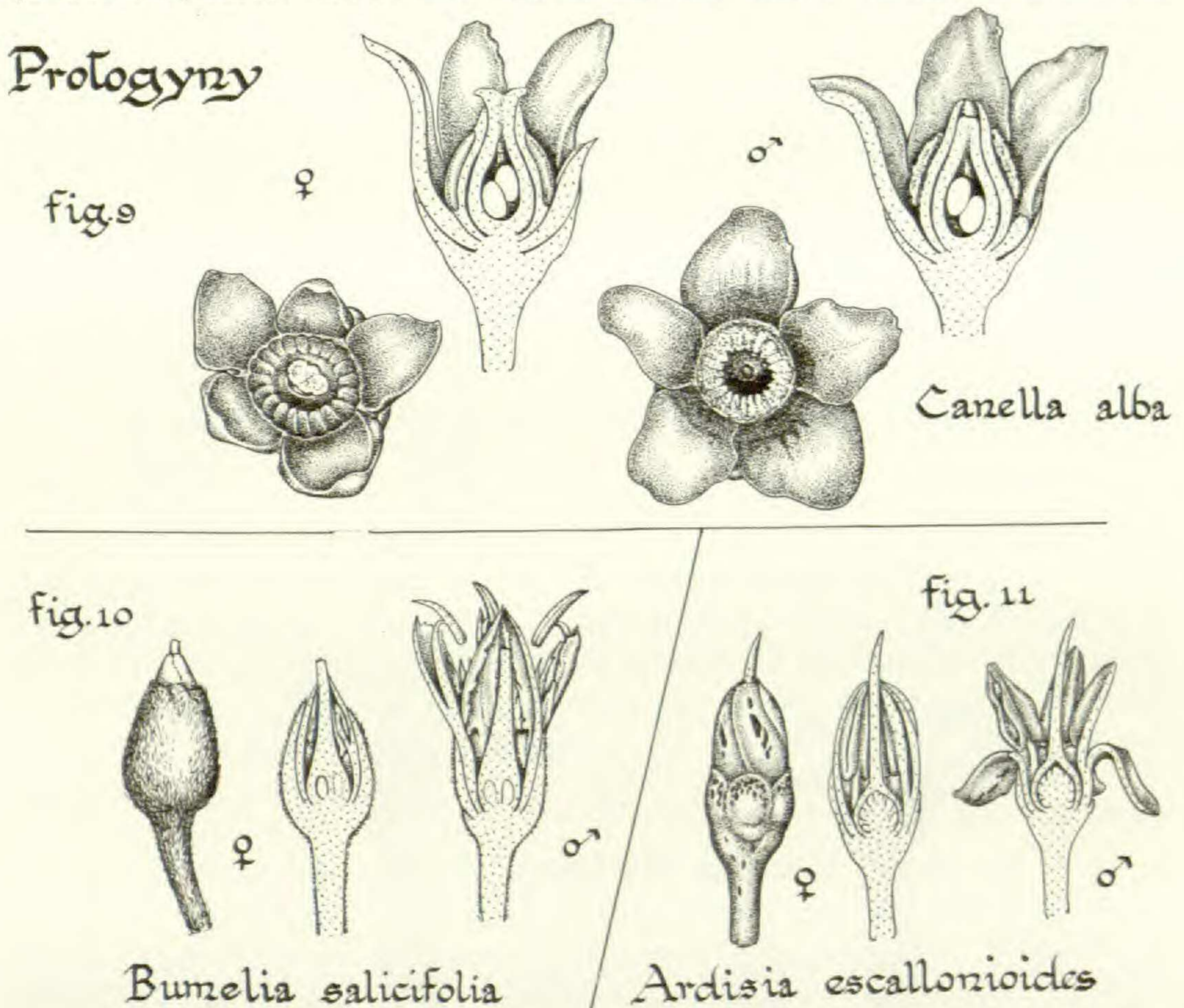
Protogyny in Lauraceae is likely to be complex in view of the known situation in avocado, as outlined earlier. Both common native species of *Nectandra* and *Persea* have essentially the same floral structure as *Persea americana* and are evidently protogynous, with the carpellate phase (stigma erect - receptive; stamens depressed - undehisced) followed by one



or two staminate phases (stigma shrivelled; stamens erect and dehiscent via pores). There may be two distinct staminate phases, with the inner series of stamens dehiscing before the 2 outer series. Wood (1958; p. 331) has observed the same precise method of dianthesis in *Persea borbonia* (near Brooksville, Hernando County) as has been described for *P. americana*. In South Florida the mechanism seems less precise, as flowers at both staminate and carpellate phases have been observed on a single tree. However, the mechanism is known to be influenced by the weather, and detailed observation is needed.

*Annona glabra* and *Magnolia virginiana* (Magnoliaceae) are both clearly protogynous, a feature common in the magnolialian families (Wood, 1958).

*Canella alba* (Canellaceae) shows the protogynous condition very clearly. When the flower first opens, the stamens, which form a continuous cylinder, remain undehiscent while the stigma protrudes and is receptive (FIGURE 9, left). Later the stigma shrivels and is retracted while the



FIGURES 9-11. EXAMPLES OF PROTOGYNY: 9, *Canella alba*,  $\times 4\frac{1}{2}$ , flowers from above and in longitudinal section, left-hand pair at early (carpellate) phase, right-hand pair at later (staminate) phase; 10, *Bumelia salicifolia*,  $\times 4\frac{1}{2}$ , flowers from the side and in longitudinal section, left-hand pair at early (carpellate) phase, right-hand flower at later (staminate) phase; 11, *Ardisia escallonioides*,  $\times 3$ , flowers from the side and in longitudinal section, left-hand pair at early (carpellate) phase, right-hand flower at later (staminate) phase.



anthers dehisce extrorsely (FIGURE 10, right). Since the pollen, when released, is conspicuous on the stamen cylinder, the distinction between the early (carpellate) and the later (staminate) phase is easily recognized. Protogyny in *Avicennia* and *Tetrazygia* is less obvious but seems distinct. The complex protogyny of *Ficus* is described in detail later (p. 283).

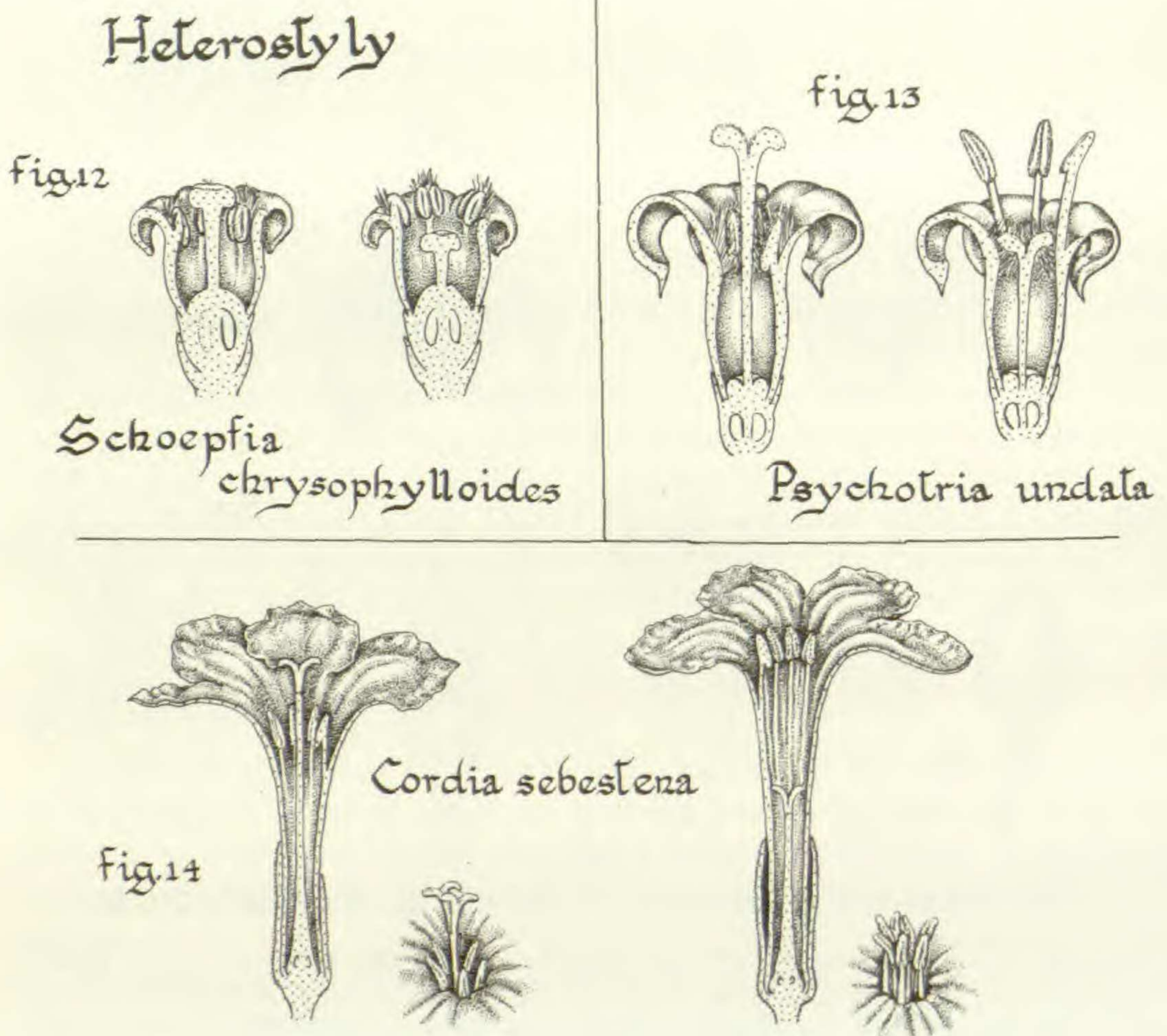
3b. *Species with dimorphic (heterostylous) flowers* (only one kind of flower on a particular individual).

CORDIA SEBESTENA (FIGURE 14)  
PSYCHOTRIA SULZNERI

PSYCHOTRIA UNDATA (FIGURE 13)  
SCHOEPFIA CHRYSOPHYLLOIDES  
(FIGURE 12)

These species all represent clear-cut examples of morphological flower dimorphism, but it is not known if this dimorphism is correlated with self-incompatibility.

*Schoepfia chrysophylloides* (Olacaceae) provides a clear-cut example of heterostyly (FIGURE 12). Previous descriptions of this species in South



FIGURES 12-14. EXAMPLES OF HETEROSTYLY; flowers in longitudinal section with long-styled form to left, short-styled form to right in each example: 12, *Schoepfia chrysophylloides*,  $\times 4\frac{1}{2}$ , left-hand flower tricarpellate; 13, *Psycho-*



Florida have not recorded it as heterostylous and, indeed, heterostyly was not recorded for the family Olacaceae by Vuilleumier (1967). However, Adams (1972) records heterostyly in *Schoepfia chrysophylloides* in Jamaica, which suggests that it is a feature of the species throughout its range.

*Psychotria* in South Florida shows heterostyly of the classical type, which is well known in the genus and in other members of the Rubiaceae. Here the floral dimorphism is always clear cut (e.g., FIGURE 13). In some other Rubiaceae in South Florida flowers are polymorphic, suggesting incipient heterostyly. These examples are included in the next category.

Heterostyly is known in species of *Cordia* (Vuilleumier, 1967). Its existence in populations of *Cordia sebestena* may account for the low fruit set of this species, which tends to occur infrequently and as isolated individuals. Distinct "pin" (long-styled) and "thrum" (short-styled) forms are here illustrated (FIGURE 14), but there is some variation in style length among individual trees of the same flower type.

#### 4. Species with polymorphic flowers, including polygamo-monoecious or -dioecious (usually more than one kind of flower occurring on a single individual).

BURSERIA SIMARUBA (FIGURE 16)

DODONAEA VISCOSA

EXOTHEA PANICULATA

GUETTARDA SCABRA (FIGURE 17)

MAYTENUS PHYLLANTHOIDES

MYRSINE FLORIDANA

PRUNUS MYRTIFOLIA (FIGURE 6)

RANDIA ACULEATA (FIGURE 15)

This is a rather artificial category, in which various kinds of floral variation are included.

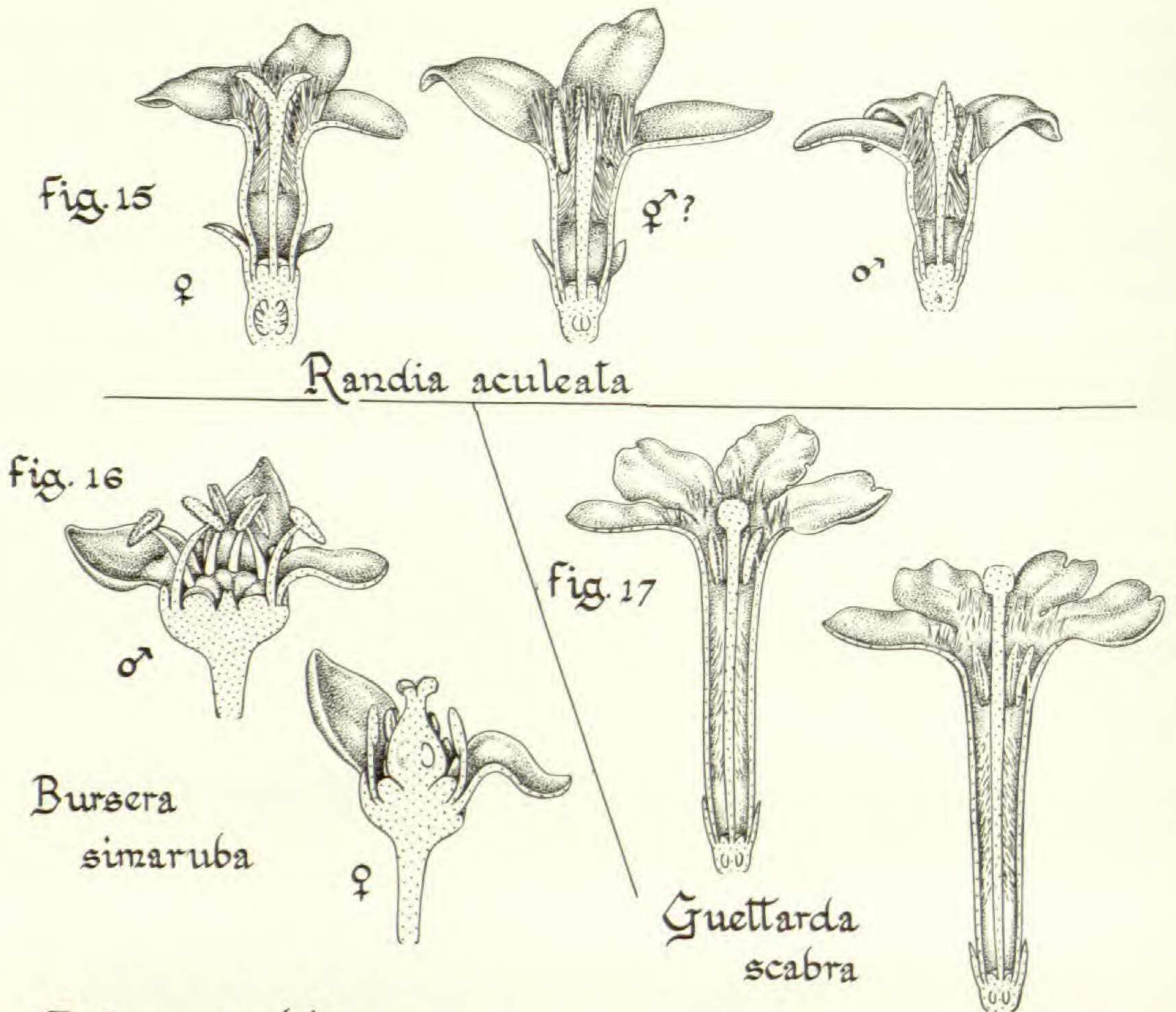
Species listed in other categories but which show some degree of morphological variation might well be included in this list, such as *Acer rubrum* and especially other members of the Sapindaceae, a family in which floral polymorphism is well known (Radlkofer, 1933). The inclusion in this category of the South Florida members of the family (*Dodonaea*, *Exothea*) is undoubtedly quite arbitrary and further field study is needed. The significance of such polymorphism in pollination and breeding mechanisms is not known.

*Bursera simaruba* (Burseraceae) is similar. Staminate and carpellate flowers are illustrated in FIGURE 16. The species is usually described as dioecious. However, I have seen no trees which seem incapable of forming fruit, as would be the case if there were staminate trees. This might reflect the limited size of my sample, since Dr. K. J. Bawa has informed me of fruitless trees of *Bursera simaruba* in Costa Rica. Perfect flowers can be found. Dr. Carroll E. Wood, Jr., has made observations which suggest that there are at least staminate and carpellate inflorescences, but

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*tria undata*,  $\times 1$ ; 14, *Cordia sebestena*,  $\times 1$ , insets show mouth of corolla tube from above in each type of flower.





## Polymorphism

FIGURES 15-17. EXAMPLES OF FLORAL POLYMORPHISM; flowers in longitudinal section: 15, *Randia aculeata*,  $\times 3$ , carpellate flower to the left, staminate flower to the right, central flower apparently perfect, but ovules probably not functional; 16, *Bursera simaruba*,  $\times 6$ , staminate and carpellate flowers representing the extreme forms; intermediates which may be described as "perfect" can occur; 17, *Guettarda scabra*,  $\times 3$ , two examples of flowers with different style lengths; this may represent incipient heterostyly.

that each staminate inflorescence usually has one perfect flower. The situation deserves more critical study.

*Maytenus phyllanthoides* (Celastraceae) has essentially perfect flowers in South Florida, but by abortion unisexual flowers are commonly produced on a single individual. It is commonly described as either monoecious or dioecious (Brizicky, 1964). The distribution and function of these flowers require further study.

The two rubiaceous species in the above list are polymorphic but not heterostylous. In *Randia aculeata* dioecism seems to predominate, since flowers on a single plant are chiefly unisexual by abortion (FIGURE 15, left and right), but the details of distribution of different flower types remain unknown. Flowers which possibly are perfect exist; these include



apparently functional stamens and a partially developed ovary with some ovules (FIGURE 15, center). Whether these flowers can set fruit is not known. In *Guettarda scabra* most of the variation is in the length of the style, without any obvious variation in the structure of the ovary (FIGURE 17). As illustrated, this variation might suggest different stages in the elongation of the style, but style length is constant for an individual flower. Number of floral parts also varies widely with whorls of four to eight members.

*Myrsine floridana* (*Rapanea guianensis* sensu most authors) resembles *Randia* in that it seems to be essentially dioecious, but apparently perfect flowers can occur. The dioecious state is best demonstrated by the observation that trees are either heavy fruit bearers, or not, but the distinction is not sharp.

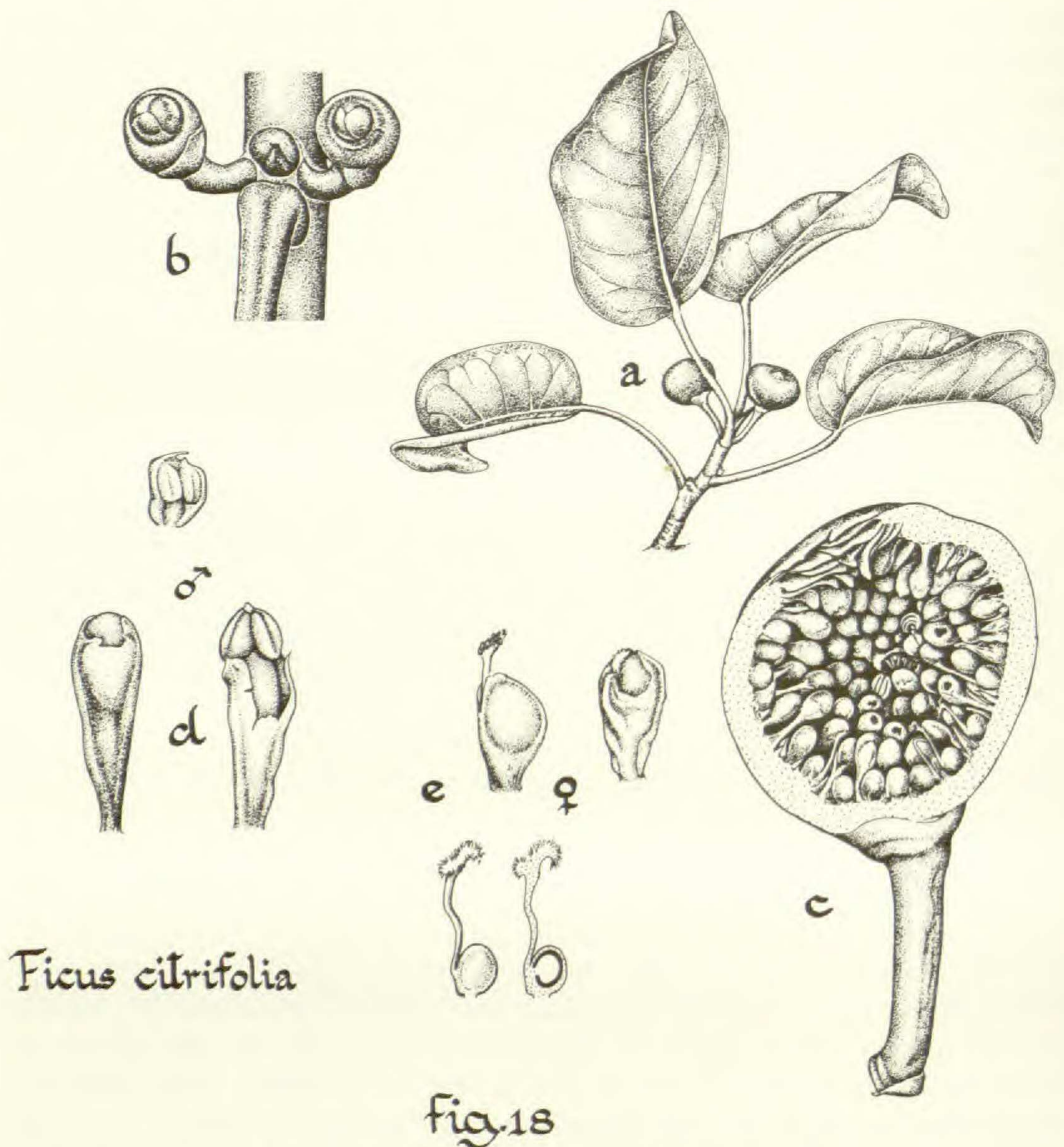
*Prunus myrtifolia* (Rosaceae) represents a species which is easy to categorize, since it is essentially andromonoecious (FIGURE 6) with separate perfect and staminate flowers on the same tree and indeed in the same spike. The basal flowers of one spike are staminate and the distal ones perfect; consequently fruits always appear toward the ends of the inflorescences.

#### THE SPECIAL POLLINATION MECHANISM OF *FICUS* SPECIES NATIVE TO FLORIDA (FIGURES 18 and 19).

The general complexity of pollination in *Ficus* is well known, and the distinctive symbiosis with species of wasps has been investigated in some detail. However, *Ficus* is one of the largest genera of flowering plants and the variations on the basic theme are many. Galil and Eisikowitch (1968) have most recently described the special mechanism in certain African species which seems to correspond to that in the two species of *Ficus* native to South Florida, *F. aurea* and *F. citrifolia*. The process is apparently the same in both species, but since different species of wasps are associated with each *Ficus* species (Galil, pers. comm.), there is no hybridization between them. The following account refers to *F. citrifolia*; *F. aurea* seems to be the same and is not described further. The general structure of the fig inflorescence and details of the flowers are shown in FIGURE 18. The mechanism is represented diagrammatically in FIGURE 19, with illustrations of male and female wasps.

The young figs (syconia) originate in pairs in the axil of a leaf on the new growth and always with a vegetative bud between them (FIGURE 18a-b). They develop within the terminal bud and are exposed by the fall of the surrounding stipules. The flowers are each subtended by a narrow bract and scattered without apparent order over the inner surface of the fig (FIGURE 18c). Carpellate flowers are either long-stalked with a short style or short-stalked with a long style in such a way that the feathery, unequal two-lobed stigmas of flowers are all at the same height (FIGURE 19a). The staminate flower consists of a single anther (FIGURE 18d). All flowers are at first enclosed in a membranaceous "perianth," which is ruptured as the flower enlarges (FIGURE 18d, right). Carpellate





*Ficus citrifolia*

Fig. 18

FIGURE 18a-e. *Ficus citrifolia*, inflorescence and flower morphology: a, leafy branch with figs,  $\times 2/3$ ; b, young fig-pair with intervening vegetative bud in axil of leaf,  $\times 4$ ; c, fig in vertical section at stage with grubs hatching,  $\times 4$ ; d, individual staminate flowers,  $\times 12$ , various ages, oldest flower (lower right) with ruptured perianth; e, individual carpellate flowers,  $\times 12$ , various ages, lower flower with perianth removed and in longitudinal section.

flowers function much earlier than staminate flowers in a way which is closely related to the method of pollination.

Female flowers expand their stigmas within the young green fig. At this stage winged female wasps (*Blastophaga* sp.), bearing fertile eggs, fly to the figs, which they penetrate via scales at the mouth that loosen slightly (FIGURE 19a). It is not known what attracts the wasps to a fig, but a chemical substance is probably involved. To enter a fig is a difficult task for such a small insect and the wasp usually loses its wings (and even its antennae) in wriggling between the scales. The remains of wasp wings among the scales will indicate that a young fig contains wasps. Once in-

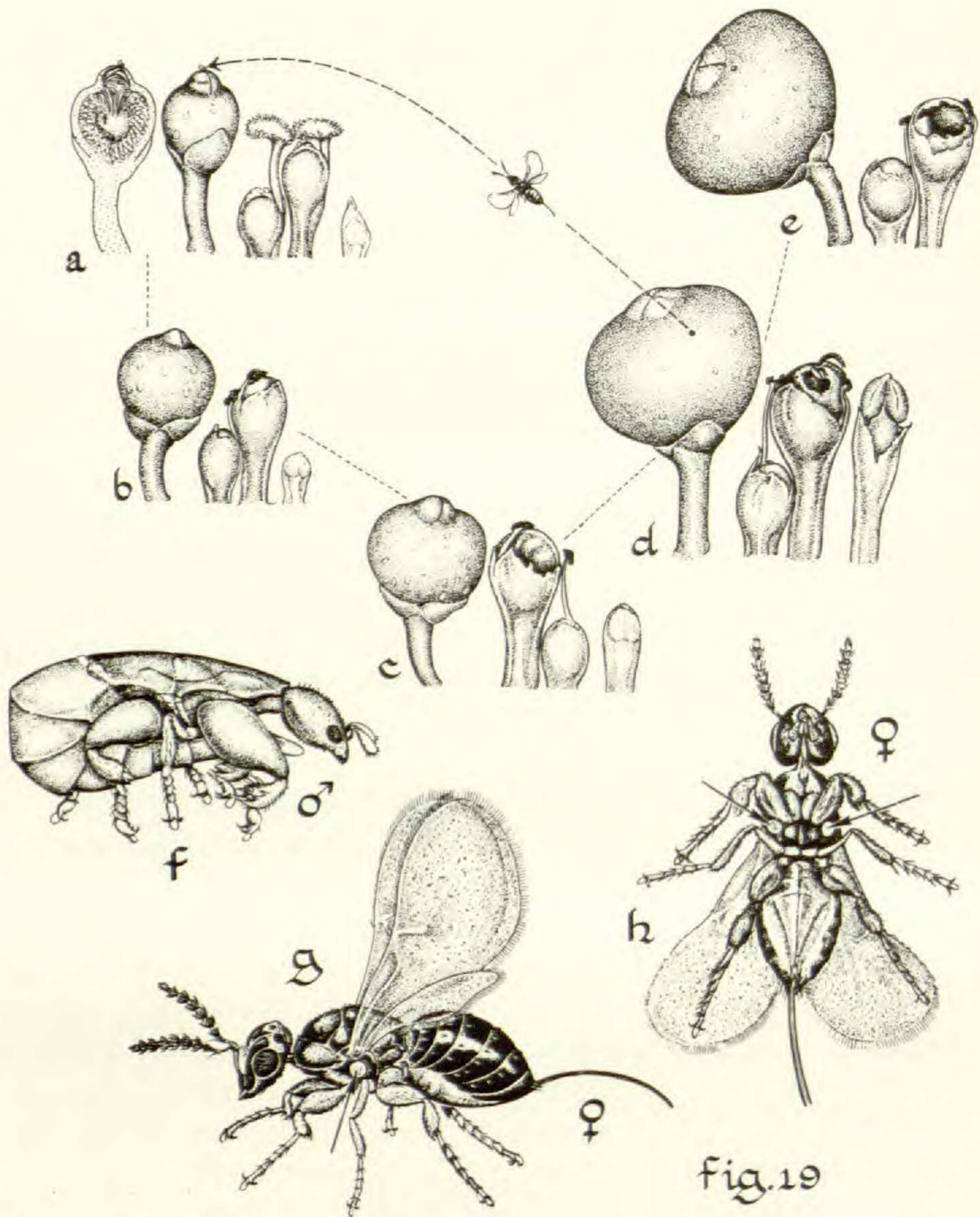


side the fig the female wasp serves her own ends by laying fertile eggs within the female fig flowers by inserting her ovipositor down the style of the flower. At the same time she actively pollinates the flower, transferring pollen to each stigma as she lays an egg. The pollen is carried in a pair of small pollen sacs, one on each side of the thorax (arrows in FIGURE 19g, h). Once egg-laying and pollination are completed the wasp dies, being unable to escape from the fig.

Female flowers, now pollinated, develop over a period of a few weeks (FIGURE 19b). Some flowers develop normally and produce a single seed; others, known as gall-flowers, produce a wasp-grub which lives on the developing ovule of the female flower. This ovule fails to become a seed. Whether a flower develops a fruit or becomes a gall-flower is determined simply by the length of its style. In short-styled flowers the ovipositor of the wasp can reach the ovule and the wasp egg develops within nutritive tissue. In long-styled flowers the wasp's ovipositor is too short to lay the wasp egg in the correct position near the base of the flower, so the egg dies. Pollination has been performed by the wasp, however, and seed development proceeds normally. It seems necessary for both types of flower to be pollinated, even the gall-flower, since the development of the ovule must take place in order that the wasp-grub may be nourished.

Figs enlarge but remain green as seeds ripen and grubs mature (FIGURE 19c). The male flower then expands, rupturing its perianth, and the stamens dehisces (FIGURE 19d). At the same time the grubs (presumably after suitable metamorphosis) hatch from the gall-flowers to produce male and female wasps (FIGURE 19f-h). The male wasp is strikingly different from the female; it is larger, wingless, and brown rather than black (FIGURE 19f). It shows evidence of paedomorphism. Nevertheless it has two important functions. First it impregnates the adult female within the flower, subsequently assisting the escape from the flower of the delicately winged female by chewing a hole in the gall-flower. Since grubs are likely to be the progeny of several different parental wasps which all entered the same fig, outcrossing between wasps can take place. Secondly, the male wasp provides a further escape tunnel for the impregnated females by eating a hole through the wall of the fig using its well-developed mouth parts. The males may themselves escape through these holes, but since they are wingless they fall to the ground and die. The females, now egg-bearing, have one important function before they leave a fig. They load their pollen sacs from the pollen provided by the ripe anthers. Details of how this is done are still unknown, and it seems (FIGURE 19g, h) that the anther does not dehisce but is bitten into by the wasp. Once pollen-loading is accomplished the females make their escape via the holes provided by the males, fly to a young fig, and begin a new cycle (FIGURE 19d). The deliberate transfer of pollen by female wasps is a peculiarly instinctive action, but one on which the whole process is dependent. Of interest is the method of survival of wasp populations during a long period in winter when *Ficus* is inactive and produces few figs. This has not been investigated.





### *Ficus citrifolia*

FIGURE 19a-e. *Ficus citrifolia*, diagram of pollination mechanism. Sequence of events, each illustration showing a fig to the left and an enlarged diagram of a carpellate and staminate flower to the right as they appear at this phase of development: a, fig recently occupied by a female wasp, carpellate flowers ready for pollination and oviposition; b, development of seed (left) and gall (right) flower from two kinds of carpellate flowers; c, ripening of seed and gall-flower; d, hatching of gall-flower and maturation of staminate flower, release of winged female insects; e, fruit ripening, empty gall-flowers. f-h. *Blastophaga* sp., male and female pollinating wasps: f, *B. sp.* male,  $\times 45$ ; g, *B. sp.* female from the side,  $\times 40$ ; h, *B. sp.* female from below,  $\times 40$ , arrows indicating position of pollen-bearing pouches.

Unfortunately the situation is complicated by a number of other insects which parasitize the fig-wasp environment. Commonly there are male and female wasps of a second species in the figs. The female of this species has a long ovipositor and it may lay its eggs in female flow-



ers without ever entering the fig so that it is of no value to the fig in pollen transfer. Additional large galls are also common in these figs, and they are probably made by an insect which enters and leaves a flower without ever going into the cavity of the fig at all.

## DISCUSSION

### DISTRIBUTION OF BREEDING MECHANISMS

The possibility that many South Florida trees are self-incompatible without there being any marked floral dimorphism is very likely in view of the high incidence recorded by Bawa (1973) in Costa Rica. Bawa records self-incompatibility for species in the genera *Manilkara*, *Piscidia*, and *Pithecellobium*, which are represented in South Florida.

In contrast *Byrsonima crassifolia* is recorded by Bawa as self-compatible. *Byrsonima lucida* in South Florida has conspicuous flowers which pass through several color phases as they develop. Assuming that this species is also self-compatible, outbreeding here may be dependent on specialized pollinator behavior but remains uninvestigated.

Since the flora of South Florida has been examined neither in detail nor experimentally, the only suggestion we presently have for outcrossing mechanisms comes from a knowledge of flower structure alone. Morphologically, out of 114 species 31 (27 per cent) are dioecious where outcrossing is obligate. Monoecism, which may promote outcrossing, occurs in 14 species (12 per cent). Heterostyly is distinct in 4 species (3.5 per cent), dichogamy is suggested in 18 species (16 per cent), and floral polymorphism, which may presage dioecism or monoecism, is evident in 8 species (7 per cent). Whether these structural differences in fact do reflect a tendency toward outcrossing can only be determined by further study. Even at the morphological level our records are very incomplete.

A further example will show that self-incompatibility and outcrossing may be more widespread than is currently evident. In the family Rhamnaceae, Galil and Zeroni (1967) have demonstrated a type of dichogamy in *Zizyphus spina-christi* which bears comparison with that in *Persea americana*, except that the flowers are protandrous, not protogynous. In *Zizyphus* Galil and Zeroni recognized 6 distinct flower phases (A-F) through which each flower passes. Pollen is presented in the earlier (staminate) phases B-C; the stigma becomes receptive in the carpellate phases D-E when all pollen is dispersed. All flowers on a single tree are in phase with each other. Outcrossing is obligate because the flowers are self-incompatible. Crossing is possible because there are two kinds of trees, staggered with respect to flower phase so that there are some trees with flowers in the male phase and other trees with flowers in the female phase.

*Colubrina* species in South Florida have flowers very similar to those of *Zizyphus*, and certain of the phases described by Galil and Zeroni can be recognized. It will be of interest to see if further work demonstrates a *Zizyphus* type of mechanism in *Colubrina*, or indeed in other Rhamnaceae.



## POLLINATION MECHANISMS

The preceding outline has been presented, except in *Ficus*, without any consideration of the probable mechanism of pollen transfer itself. Initially one can make a rather subjective distinction between wind- and insect-pollinated flowers. Probable wind-pollinated species are marked with an asterisk in the preceding tables, based largely on flower structure and pollen texture. Most doubt can be cast upon my claim for wind pollination in the tropical level. However, even at this subjective level the incidence of wind-pollinated species is low. Furthermore, wind-pollination is strongly correlated with dicliny, on the one hand, and a temperate distribution, on the other. Of the 45 species included in the dioecious and monoecious category, I estimate that 15 (33 per cent) are wind-pollinated, whereas probably no species<sup>2</sup> with perfect flowers is wind-pollinated (0 per cent). A proportion of species with a generally temperate distribution (marked \* N in the above tables) are wind-pollinated (4 out of 7 of the dioecious species; 4 out of 4 of the monoecious species). This confirms the higher incidence of wind-pollination in temperate tree floras which is generally appreciated and has been discussed recently by Daubenmire (1972), Janzen (1967), and Whitehead (1969) in relation to such factors as availability of pollinators, deciduousness, and the distribution of angiosperm families.

## PHENOLOGY

Interaction between flowering trees and pollinators implies a close dependence on their respective seasonal behavior, as had been emphasized by Janzen (1967). It is perhaps not justifiable to comment upon seasonal flowering behavior of trees in South Florida, since the subject is scarcely investigated and my own phenological records are too incomplete to indicate more than general trends. However, the subject is of major importance in a discussion of breeding mechanisms in trees. Observations made so far show that many trees have distinctive (though often extended) flowering periods and that published records of trees as "ever-flowering" are often misleading, in part because they are based on early literature which was produced by observers who had little opportunity to make continuous records. The subject needs long, continued field investigation.

Diurnal variation in flower function is also an important factor in the study of pollination and breeding mechanisms. In certain trees in South Florida the flowers open only at night (e.g., *Capparis* species) or become scented at night, notably *Mastichodendron foetidissimum*. The pollinating agents here are not known.

These brief comments serve to indicate the several directions from which the observer may proceed once a more complete morphological assessment has been made.

<sup>2</sup> Recent field observations by John W. Kress (Harvard undergraduate) suggests that *Rhizophora mangle* is wind-pollinated and that populations of this species include male sterile plants. Statements about this species may have to be modified.



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HARVARD FOREST

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